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DISPLAYS OF THE MAGELLANIC OYSTERCATCHER (*HAEMATOPUS LEUCOPODUS*)

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The Magellanic Oystercatcher (*Haematopus leucopodus*), endemic to southern South America, has a curious combination of features of New and Old World Haematopodidae. It has yellow eyes and pale legs, like the New World Blackish (*H. ater*), Black (*H. bachmani*) and American (*H. palliatus*) oystercatchers, contrasting with the scarlet eyes and pinkish-red legs of other oystercatcher species (Strauch 1976). *H. leucopodus* resembles Old World *Haematopus* spp., however, in lacking a brownish cast to its black dorsal plumage. Moreover, it is unique in having yellow orbital rings, which are orange in other *Haematopus* spp., and in having underwing coverts of a different color than the belly plumage (Strauch 1976).

H. leucopodus is also unusual ecologically. Most nest inland on the pampas of Argentina, often far from marine littoral habitats. Some populations of the European Oystercatcher (*H. ostralegus*) also nest inland in extensive natural open habitat.

Despite its unusual characteristics *H. leucopodus* is poorly known. We gathered data on its behavior during 1 nesting season, in conjunction with ongoing ecological and systematic studies on the Haematopodidae (Baker 1974, 1975, 1977). We describe some of its visual and vocal displays, particularly piping displays and displays of adults disturbed near the nest or with chicks. We include comparative observations on *H. ater* and on the Patagonian and eastern North American races of the American Oystercatcher (*H. palliatus durnfordi* and *H. p. palliatus*, respectively).

METHODS

We studied *H. leucopodus* about 85 km NW of Rio Gallegos, Argentina, from 1-10 November 1977. We observed *H. ater* and *H. p. durnfordi* at Punta Tombo, Argentina, on 12

and 15 November, and *H. p. durnfordi* at Punta Ninfas, Argentina, on 14 November. Baker also studied a population of color-banded *H. p. palliatus* at Wallops Island, Accomac Co., Virginia, during the 1978 and 1979 nesting seasons.

Motion pictures of *H. leucopodus* and *H. p. palliatus* were taken with a Bolex 16 mm camera at 24 frames/sec. Most tape recordings were made at 19 cm/sec with a Nagra IS tape recorder on Scotch 208 tape, matched to the Nagra, using a Sennheiser MKH 816 microphone with wind sock. Recordings in Virginia were taped at 19 cm/sec on a Uher 4200 Report Stereo IC tape recorder on Scotch 208 tape, using a Uher M517 dynamic microphone mounted in a Dan Gibson parabolic reflector. Sonagrams and amplitude profiles were prepared on a Kay Elemetrics Sonagraph 7029A with amplitude display/scale magnifier unit 6076C. Its frequency calibration was checked against pure frequencies from a signal generator. Time markers are based on the revolution time of the drum (2.55 sec over the range 80–8000 Hz, for the machine used).

We sexed oystercatchers on the basis of the relative sizes of mates and relative bill color. Males average smaller than females in all oystercatcher species, and male *H. ostralegus* in Europe and Australasia are nearly always smaller than their mates (Heppleston and Kerridge 1970; A. J. Baker, unpubl.). Additionally, bill color in breeding males of most or all species is decidedly richer and pinker than in females; their bills seem dull orange by comparison. This sexual difference in bill color was also apparent in 22 copulating pairs of *H. p. palliatus* and in collected specimens of the 4 taxa.

OBSERVATIONS

Tail-flagging.—Adult *H. leucopodus* gave various distraction displays when disturbed near the nest. The most striking display is tail-flagging. A typical display proceeds as follows (Fig. 1A, E): The bird rose from its nest with its neck retracted (note prominence below nape, Fig. 1A, frame 1 [f1]); then turned and walked slowly from the nest with contour feathers sleeked and head and neck low, but with feathers around the vent slightly erected (f46). It then quickly raised its tail (f46–62), exposing the underside of the tail toward us while erecting and spreading the under-tail coverts (f62, 73). It walked slowly or was nearly motionless in this posture. Movement of the wings away from the body began in f46, after which they were conspicuously fluffed and drooped. A similar sequence recurred within seconds, but the bird assumed a low crouched posture with lifted tail (e.g., f173), and it trod quickly on the spot while shuffling its fluffed, drooped wings. Treading usually ceased when an upright posture was assumed (f231, as in f73). The female in Fig. 1E turned toward us and leaned forward with tail up and wings fluffed and drooped (third and fourth sketches). The white chevron at the base of her tail was fully displayed and much of the tail was conspicuously framed by the under-tail coverts (fourth sketch).

False-brooding and other lure displays.—Less striking displays include crouching with sleeked plumage, slight drooping, fanning or rotation of the tail, and lowered wings kept fairly close to the body (note lowered wing tips below tail, Fig. 1B, f1–188). These low intensity postures sometimes

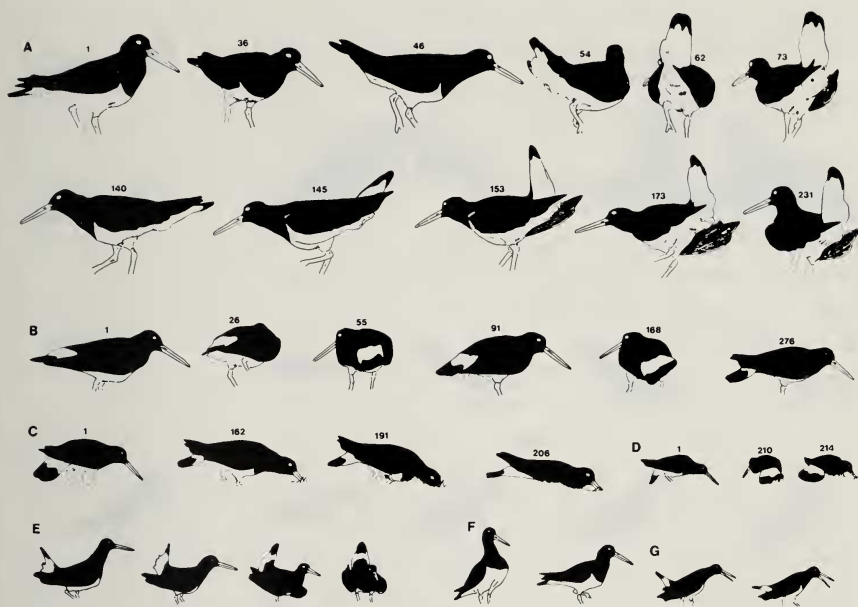


FIG. 1. Postural displays of *H. leucopodus* disturbed near the nest (female throughout). Numbers in A–D refer to frame numbers from movies. Parts E–G are from still photographs. (A) Rising from nest and performing 2 tail-up displays; (B) farther from nest; (C) still later, farther from nest, false-brooding (after fl); (D) still later, farther from nest; (E) another female in display a few seconds after she left nest; (F) this female immediately after landing near nest, then walking toward it; (G) this female near nest, walking slowly, while piping in response to distant piping.

merged into sequences of false-brooding (Fig. 1C, f162–206) or crouches with the tail depressed and fanned (Fig. 1D). Birds like those in Fig. 1B and 1D generally walked slowly and haltingly away from us; the bird in Fig. 1D also stopped and remained motionless for long periods. False-brooding birds remained in place briefly while acting as though settling on a nest.

We saw many *H. ater* and *H. p. durnfordi* near their nests. Most remained nearby while calling loudly, but a few *H. p. durnfordi* false-brooded weakly. Neither species exhibited tail-flagging or other lure displays. False-brooding occurs in *H. bachmani* (J. P. Myers, in litt.). Territorial *H. bachmani* sometimes crouch with depressed tail during aggressive interactions (S. Groves, in litt.).

Piping.—Piping is a common and conspicuous display in all species of oystercatchers. It involves loud calls and striking postures and move-

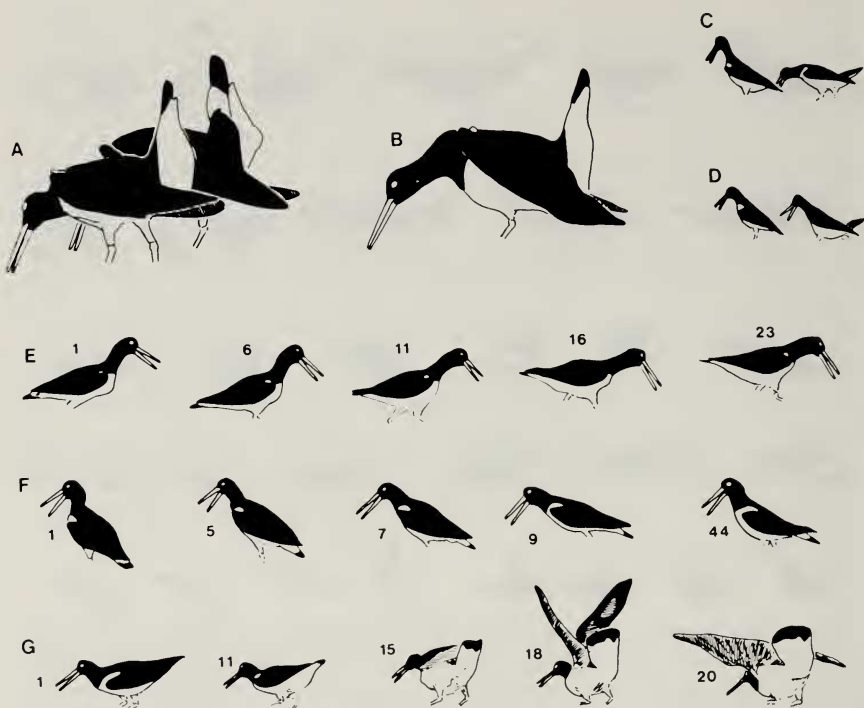


FIG. 2. Postures during piping displays in *H. leucopodus* and *H. p. palliatus*, and displays by a male *H. p. palliatus*. A and B are from still photographs. Numbers in parts E–G refer to frame numbers from movies. (A) Pair of *H. leucopodus* piping with a neighboring pair (not shown); (B) *H. leucopodus* piping with its mate and a neighboring pair (later in the same sequence as A); (C, D) *H. p. palliatus* piping; (E, F) female *H. p. palliatus* piping while walking rapidly toward a neighbor who was circling low over her nesting territory; (G) male *H. p. palliatus* piping while squatting, then raising his wings and tail as a neighboring male swooped down toward him; the intruder apparently struck this male in f27.

ments, and is usually given in aggressive and sexual contexts at close range on the ground. Piping is given less commonly in flight.

Piping in *H. leucopodus* was commonest during territorial demarcation, and involved 1 or both members of neighboring nesting pairs. For example, a nesting pair of *H. leucopodus* engaged their neighbors in piping interactions several times over 2 days of observations. Piping recurred along a stretch of barbed wire fence, with the pairs separated by a few meters on opposite sides. Mates generally remained close together during such encounters (e.g., Fig. 2A). One pair piped when they were reunited with their 2-week-old chick after we released it. Piping also occurred when

mates rejoined after an absence, especially if one of them had just engaged in piping elsewhere. Following piping displays with neighbors, birds often piped while flying over their territory or after landing there. One male piped as he flew close to the nest to relieve his mate; the female piped as she flew away after changeover (time elapsed, ca. 8 min). Another pair piped in flight after following a hawk which passed through their territory.

During piping on the ground, *H. leucopodus* lifted the wings slightly out from the body (especially at the carpal flexure), erected the tail until it was roughly vertical, fanned the under-tail coverts and lowered the head and neck. The lifting of the wings at the carpal flexure exposed the white shoulder spots (Fig. 2A, B). The head and neck remained lowered with the bill pointing down throughout high intensity portions of piping interactions (e.g., Fig. 2A, B). Occasionally the head was lifted up quickly with the bill still pointing down, and was held there briefly before being re-lowered. This stiff quick action was often repeated several times in succession, with brief pauses when the head was elevated and longer pauses when it was lowered. The movement strongly resembled feeding, though it was more stereotyped and the bill never touched the ground. Indeed, displacement feeding was common during pauses in aggressive piping performances and was characterized by unusually vigorous insertion of the bill into the ground and twisting movements. It was not observed in piping between mates.

Parallel running with short quick steps also accompanied aggressive piping, and was interspersed with sudden pivoting actions when the piping birds turned about 180° and ran together in the opposite direction. When running, piping birds dropped their tails 20° or more below vertical (Fig. 1G). Mates piping were not observed running and pivoting. They generally walked slowly or stood in one place.

After landing, some birds piped in an erect posture with breast feathers fluffed and the feathers on the belly sleeked (Fig. 1F). This display also occurs in *H. bachmani* (S. Groves, in litt.), and resembles one seen in the Magellanic "Plover" (*Pluvianellus socialis*; Fig. 6 of Jehl 1975).

Piping in *H. leucopodus* was highly contagious. Birds became alert upon hearing piping, and either flew piping toward the source or piped where they were (Fig. 1G). We observed up to 8 *H. leucopodus* piping together on the ground, and at least some of them had nests with eggs. Thus, piping probably has more functions than reaffirming boundaries of nesting territories. Piping lasted up to 11 min between 2 neighboring pairs.

Piping in *H. ater* and *H. palliatus* is similar to that in *H. leucopodus*. One pair of *H. ater* piped in flight after a ground performance with other birds, then piped together after landing at some mussel beds. Paired *H. ater* often piped together on the ground when conspecifics flew over their

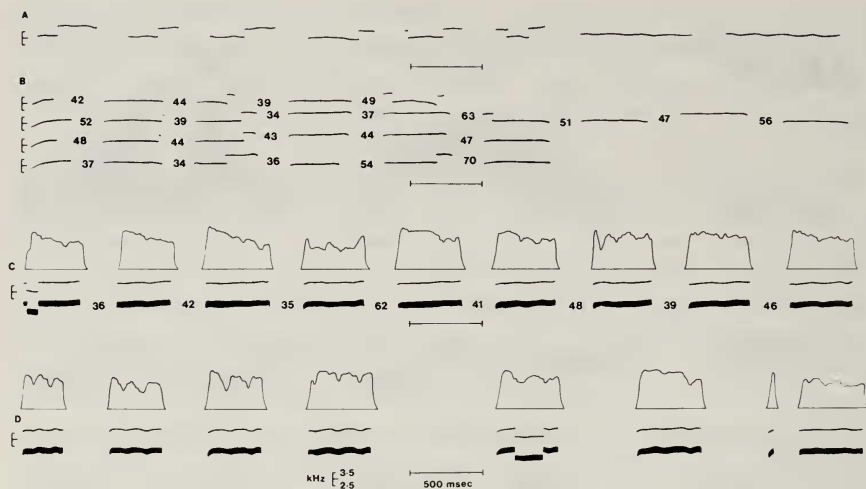


FIG. 3. Calls of *H. leucopodus* disturbed near the nest. (A) Eight calls (not in sequence of occurrence, intervals are arbitrary) from 4 birds flying around us (analyzing filter band width 45 Hz); (B) 4 complete series of ground calls from a lone bird (numbers between calls indicate intervals between them in csec; analyzing filter band width, 45 Hz); (C) flight calls from 1 bird in A (amplitude profiles are above the narrow and wide band representations; numbers between calls indicate intervals between them in csec; analyzing filter band widths, 45 and 300 Hz); (D) flight calls from 1 bird of a pair (amplitude profiles are above the narrow and wide band presentations; call intervals can be estimated by the time marker; analyzing filter band widths, 45 and 300 Hz). Only the fundamental frequency of each call is shown.

nesting territory, and some pairs piped after we moved away from their nests. One male *H. p. durnfordi* started piping when joined in flight by his mate (Fig. 9B). We did not see piping between *H. ater* and *H. p. durnfordi*, though both species were nesting abundantly on Punta Tombo. However, we saw a male *H. ater* chase a passing *H. p. durnfordi* in flight, and saw a nesting bird which appeared to be a hybrid between the 2 species; its mate was a typical *H. p. durnfordi*.

During aggressive piping, *H. p. palliatus* sometimes lifted the tail weakly and briefly (Fig. 2C, D) and held the wings away from the body. Both members of a piping pair occasionally held their tails about 30° above the horizontal for several seconds (see also Kilham 1980). However, this component of piping in *H. palliatus* was less extreme than in *H. leucopodus* (Fig. 2C-F), though Kenyon (1949:198) remarks that "the tail was pointed sharply upward" in a piping *H. p. frazari*. One male *H. p. palliatus* erected and fanned his tail when a neighboring male dove at him (Fig. 2G). We did not see tail erection in *H. ater* but viewed a commercial movie about Punta

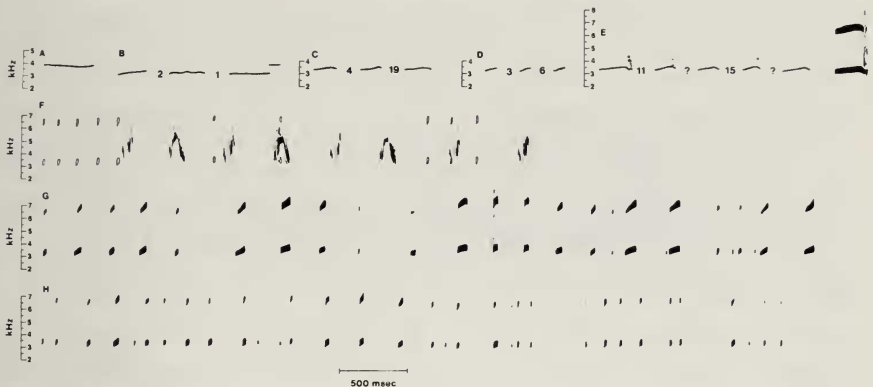


FIG. 4. Calls of *H. leucopodus* disturbed near the nest. (A) Ground call by a lone bird; (B) consecutive calls by a bird on the ground, in takeoff and immediately after takeoff; (C) ground calls by a female of a pair; (D) ground calls by 1 bird of a pair; (E) ground calls by a lone bird; (F) ground calls by a pair (male in outline, female in black); the female was in distraction display (see text); (G, H) later ground calls by the male in F.

The fundamental frequency of each call is shown, except for the wide band representation in E, and all of F-H. Numbers between calls in A-E indicate intervals between them in sec. Intervals between calls in F-H can be estimated by the time marker. Analyzing filter band width for A-E (except last call), 45 Hz, and for E (last call only) and F-H, 300 Hz.

Tombo in which piping oystercatchers purported to be this species held the tail almost vertical. Reynolds (1935) also mentions tail erection in piping *H. ater*. Piping in *H. ater* and *H. palliatus* incorporated head-up/head-down movements as described for *H. leucopodus*.

Butterfly flights.—*H. ater* and *H. p. palliatus* gave occasional “butterfly flights” in which the wings flapped slowly through an exaggerated arc (see Fig. 6 of Glutz von Blotzheim et al. 1975). All butterfly flights by *H. p. palliatus* were lone displays by birds from pairs that were incubating or had recently lost clutches. These flights were given in many circumstances, often away from territories. We do not know the breeding status of the *H. ater* which gave this display. We did not see butterfly flights in *H. leucopodus* or *H. p. durnfordi*, possibly because of the brevity of our study.

Calls by adults disturbed near the nest.—*H. leucopodus* disturbed near the nest gave various calls. Birds which stood attentively or flew near us emitted thin whistle-like alarm calls of nearly constant frequency, which often broke to higher or lower frequency (Fig. 3, 4A-E). Most of these calls were between 3 and 4 kHz, and lasted at least 0.3 sec. These loud calls occurred in fairly rhythmical series with silent intervals lasting ca. 0.5 sec, and their durations varied little (Fig. 3B-D). One bird gave several

call series, each starting with a brief call rising gently in frequency (Fig. 3B). These were followed by nearly constant frequency calls (twice with brief high frequency endings), then calls which broke to higher frequency partway through. The beginning frequency of a call is seemingly related to the terminal frequency of the preceding call. For example, in the second sequence in Fig. 1B, the third call ended at high frequency, the fourth and fifth calls continued at the same level, the sixth call started there, then shifted to a lower frequency, and the seventh call remained there.

Amplitude profiles of calls varied among individuals. One bird's alarm calls generally declined in amplitude throughout, and another bird's calls showed 3 amplitude peaks (Fig. 3C, D). These trends were not affected strongly by breaks in frequency (e.g., first call in Fig. 3C, and fifth call in Fig. 3D).

One bird ended its flight calls in wide band noise (Fig. 4E). Slow rhythmic frequency modulation (FM) coupled with amplitude modulation characterized some individuals (e.g., Fig. 3D), and occurred in certain very long flight calls (e.g., last 2 calls in Fig. 3A). Frequency modulation also occurred in calls emitted during takeoff (e.g., second call in Fig. 4B) and in calls associated with changeovers at the nest (see below). Other variants also occurred commonly, including descending frequency calls (Fig. 4A) and brief calls of rising frequency (Fig. 4C, D). The latter resemble early calls in piping series.

H. leucopodus has several other distinct types of calls. One female emitted complex noisy calls (Fig. 4F) while crouching in weak distraction display with her tail elevated to about 45°, and occasionally while false-brooding. The 2 call types she uttered were alternated; if we refer to her first and second call types in Fig. 4F as A and B, then A followed A once, B never followed B, B followed A 16 times, and A followed B 13 times. During this sequence the male stood upright and gave very brief soft "chip" calls, which were brief when delivered rapidly and lengthened when the cadence slowed (Fig. 4F, H). Some of the long chip calls resembled calls from a parent answering a chick calling in distress after we captured it (Fig. 6B). Finally, both sexes occasionally gave a "growl" call near the nest, usually while partly crouched with weak or no tail erection. Growls are wide band calls which were sometimes emitted in rapid rhythm (e.g., Fig. 5A, male in Fig. 5C), but at other times were longer, louder and less rhythmic (e.g., Fig. 5B, female in Fig. 5C).

H. ater, disturbed near the nest, gave variable loud calls (Fig. 7A, G). Some of the compound calls are comprised of rapidly delivered simple calls (e.g., second call in Fig. 7A-C, last 5 calls in Fig. 7D), and some seem to result from coalescence of simple calls (e.g., last call in Fig. 7F). Intermediate states are common (e.g., third call in Fig. 7A, second call in

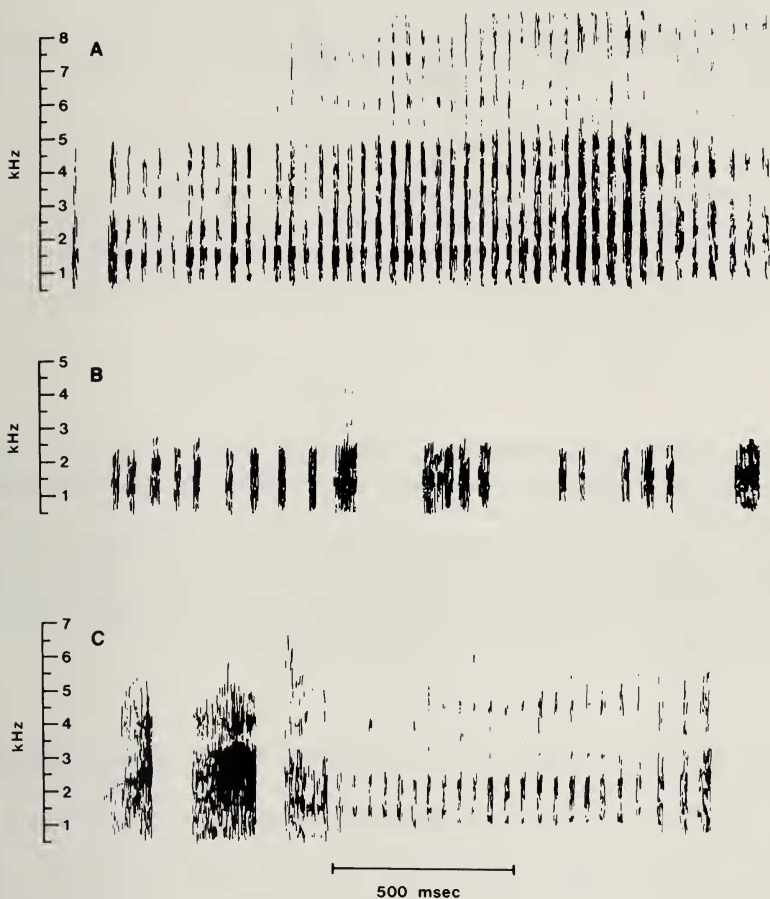


FIG. 5. "Growling" calls of *H. leucopodus*. (A) female standing upright near her nest, with tail erected about 45°; (B) different female near her mate, crouched with tail erected about 20°; (C) 3 loud bursts by the female in B, the last of which overlaps the start of a softer growling sequence by her mate, who was standing upright nearby. Analyzing filter band width, 300 Hz.

Fig. 7C). Even some simple calls show suggestions of being bi-peaked possibly through fusion or elaboration of a simple call (e.g., in Fig. 7D, E).

Calls of *H. palliatus* disturbed near the nest were similar to those of *H. ater* (Fig. 7H-P). Sonagrams for *H. palliatus* show few intermediates between simple and compound calls, in contrast to *H. ater*.

Sonagrams of calls of *H. ater* and *H. palliatus* show a sudden upward

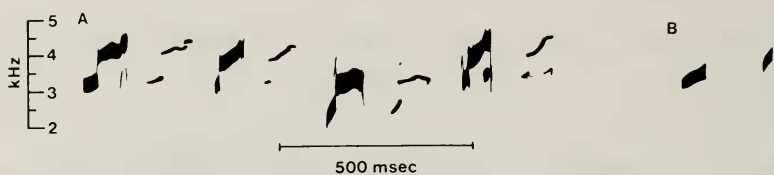


FIG. 6. Distress calls of a 2-week-old chick of *H. leucopodus* and answering calls by 1 parent. (A) Four cries by the chick while hand-held (each call shown in wide, and narrow band representation; analyzing filter band widths, 300 and 45 Hz); (B) 2 isolated ground calls by a parent of the chick, each given in immediate response to single loud calls by the chick before we released it (analyzing filter band width, 300 Hz). Only the fundamental frequency of each call is shown.

shift to a lower or higher frequency component, reminiscent of *H. leucopodus* (Fig. 7E, fourth and fifth calls in Fig. 7F, third to fifth calls in Fig. 7I, Fig. 7K-M).

Piping.—It was usually impossible to distinguish among calling birds in a piping display, for they all assumed piping postures. However, sequences of calls from piping interactions involving several birds often included sequences from only 1 or 2 birds at a time.

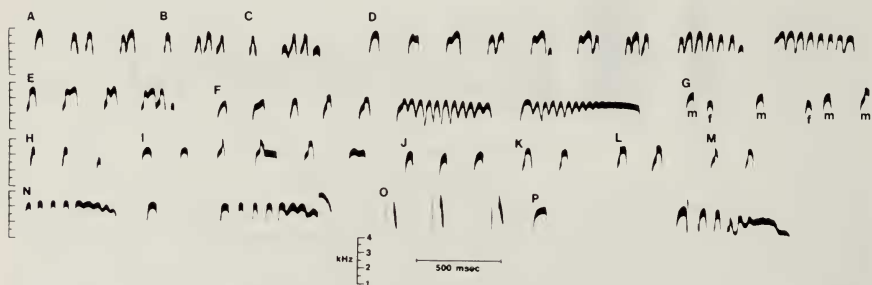


FIG. 7. Ground calls of *H. ater* and *H. palliatus* disturbed near the nest. Intervals between calls are arbitrary except where noted. Only I and N are from the same bird. (A, B, C) Three, 2 and 2 calls of *H. ater*, respectively; (D) 9 calls of *H. ater* arranged to show variation from single to bi-peaked and compound-repetitive forms; (E) 4 calls of *H. ater*, arranged as last; (F) 7 calls by a female *H. ater*; (G) calls by a pair of *H. ater* in the sequence they were given (m = male, f = female) (intervals between the first 5 calls can be judged from the time marker; the interval between the last 2 calls is arbitrary); (H-M) calls of *H. p. durnfordi*; (N) calls of *H. p. durnfordi* (the interval between the single central call and the last compound call can be judged from the time marker; the preceding interval is arbitrary); (O) 3 calls of *H. p. palliatus*; (P) 2 calls of *H. p. palliatus* (the interval between them can be judged from the time marker). Only the fundamental frequency of each call is shown. Analyzing filter band width, 300 Hz.

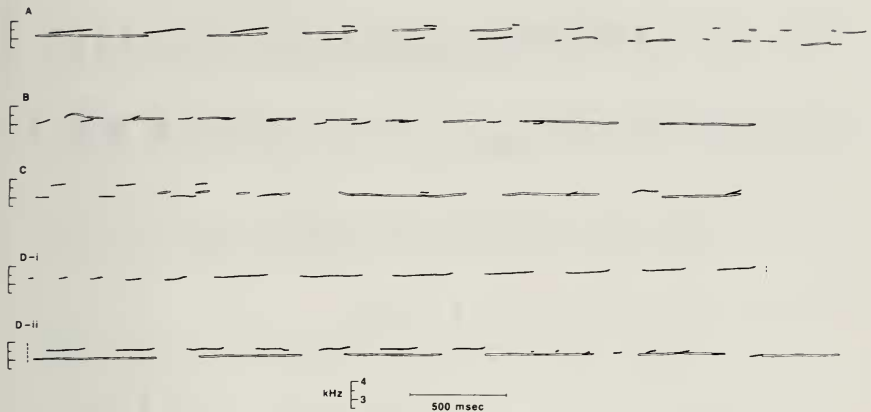


FIG. 8. Ground piping vocalizations of *H. leucopodus*. (A–C) Parts of a long piping interaction by a pair after they were joined by their chick we released (see Fig. 6) (calls of the 2 adults are distinguished in each part, but may not be represented the same in all parts); (D) part of a long piping interaction among 5 birds (vertical dashed line indicates where the 2 segments of the sequence are joined; 2 calling birds are distinguished, though at the end of part D-ii other birds started calling; their calls are not shown). Only the fundamental frequency of each call is shown. Analyzing filter band width, 45 Hz.

Piping in *H. leucopodus* began with brief calls which rose slightly in frequency and became progressively longer (e.g., Fig. 8D-i). Sometimes the calls shortened later in the series, then led into another series of brief calls (e.g., Fig. 8D-ii), or changed to a series of calls with rapid frequency shifts (e.g., both callers in Fig. 8A). Numerous other variants occurred.

Piping in *H. ater* and *H. palliatus* also began with rapid, brief calls which became progressively longer (Fig. 9–11), a trend which occasionally recurred in a single piping sequence (last part of Fig. 11E-ii). Piping in *H. p. durnfordi* and *H. p. palliatus* was similar in all respects (Fig. 9, 10). In this species the longer calls later in a sequence tended to occur in couplets (e.g., black calls in Fig. 9 near end of A-ii, B, and D-ii; outlined calls in Fig. 10C–E). This was even more pronounced in *H. ater*, and sonagrams show some calls that are fused, bi-peaked (Fig. 11A–E) and even multi-peaked (Fig. 11C-i). Long calls occurred in piping interactions in *H. ater* and *H. palliatus*, often near the beginning and end of complete sequences (Fig. 9A-i, B, C, and D-ii; Fig. 10A, E; Fig. 11E-i), though none was as long as comparable calls of *H. leucopodus*. Many brief piping calls in *H. ater* and *H. palliatus* showed sudden changes in frequency suggestive of those seen in *H. leucopodus* (e.g., most of the black calls in Fig. 9A-i;

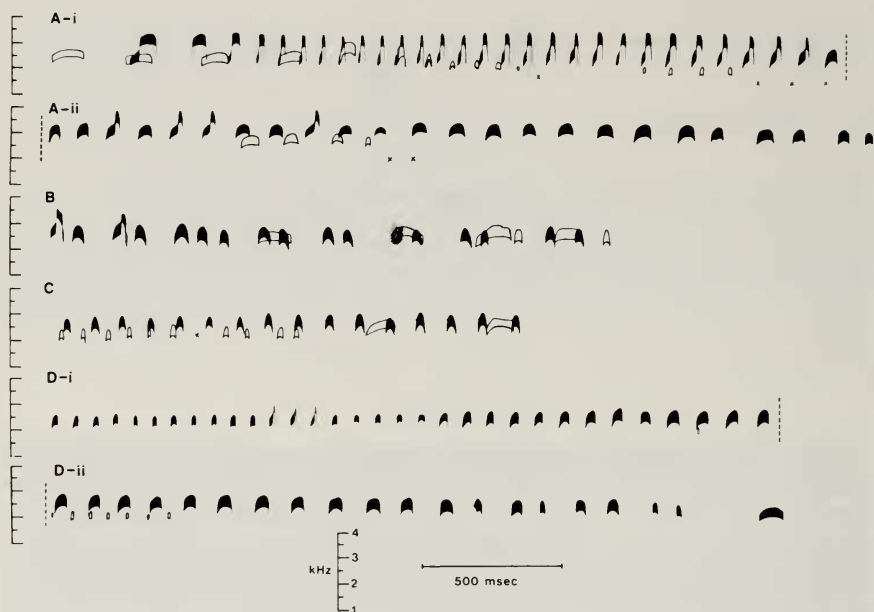


FIG. 9. Piping vocalizations of *H. palliatus durnfordi*. An 'x' or hatching indicates that a call was too faint or distorted to reproduce. (A) Nearly complete piping sequence by a male in flight (in black) and an unknown bird (only the first few calls are not shown; vertical dashed line indicates where the 2 segments of the sequence are joined); (B) segment of a piping sequence by a male in flight (in black) upon being joined by its mate (this segment starts about 500 msec after the start of calling); (C) later segment in the same piping sequence as in B, with the male's calls still shown in black (vocal component of this interaction ended about 2.5 sec after the end of this segment); (D) nearly complete piping sequence by a pair on the ground (only the first few calls are not shown). Only the fundamental frequency of each call is shown. Analyzing filter band width, 300 Hz.

third, fifth, sixth and ninth calls in Fig. 9A-ii, first and third calls in Fig. 9B; first 5 calls in Fig. 10A, etc.; most of the black calls in Fig. 11E-ii, etc.).

Many calls from piping series are very similar to alarm calls (e.g., compare calls of *H. ater* in Fig. 11A-D with those in Fig. 7A-G, and calls of *H. leucopodus* in Fig. 8 with those in Fig. 3 and 4A-E).

Other calls.—A hand-held 2-week-old chick of *H. leucopodus* gave brief calls (Fig. 6A). These involved sudden frequency shifts closely resembling those described for adult *H. ater* and *H. palliatus*, though longer.

H. ater and *H. palliatus* gave long *hueep* calls which gently rose, then fell in frequency (Fig. 11F-J), usually associated with flight (see legend to

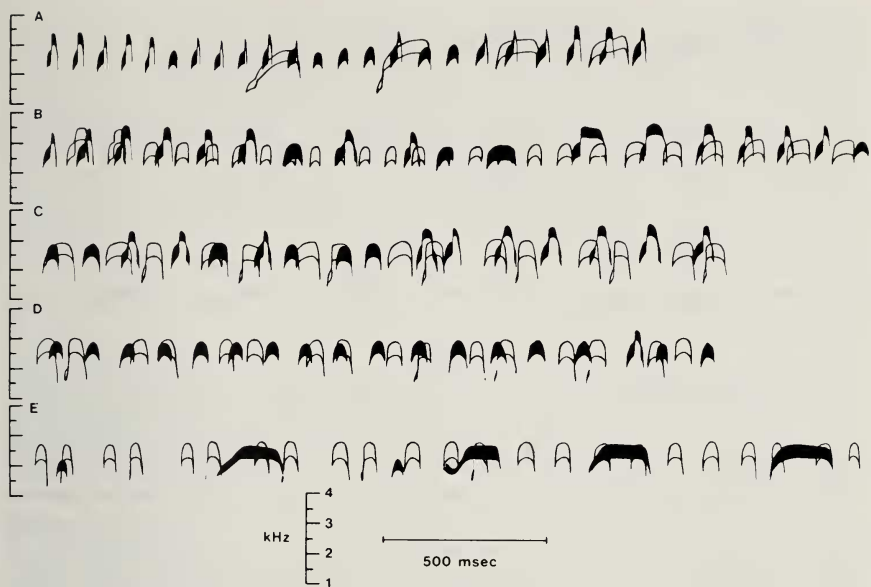


FIG. 10. Ground piping vocalizations from a piping interaction involving about 4 *H. p. palliatus*. (A) and (E) show beginning and end of a single unbroken calling sequence lasting about 23 sec; and (B–D) are segments from in between, shown in the order they occurred. Two calling birds are distinguished in each part but they may not be represented the same in all parts. Only the fundamental frequency of each call is shown. Analyzing filter band width, 300 Hz.

Fig. 11F–J). In both species, these long calls were given when 1 or 2 paired birds flew over foreign territories. We do not know if *H. leucopodus* possesses an analogous call, although undisturbed paired birds of this species flying together called often.

H. leucopodus gave many calls before or after changeover at the nest. For example, relieving birds sometimes called before and after landing, and the relieved bird often called before flying off or during its flight away. These calls all seemed to be of constant frequency and many were relatively soft. One female gave flight calls with slow rhythmic FM before and after nest relief.

H. ater, in butterfly flight, uttered a continuous series of simple notes. Our tape recordings of this call are poor, but its fundamental frequency is around 2.5–3 kHz, and its mean duration \pm SD is 23.8 ± 2.98 msec ($N = 14$). The intervals between calls are around 84.8 ± 13.34 msec ($N = 11$). Similar notes have been heard during butterfly flights of *H. palliatus*.

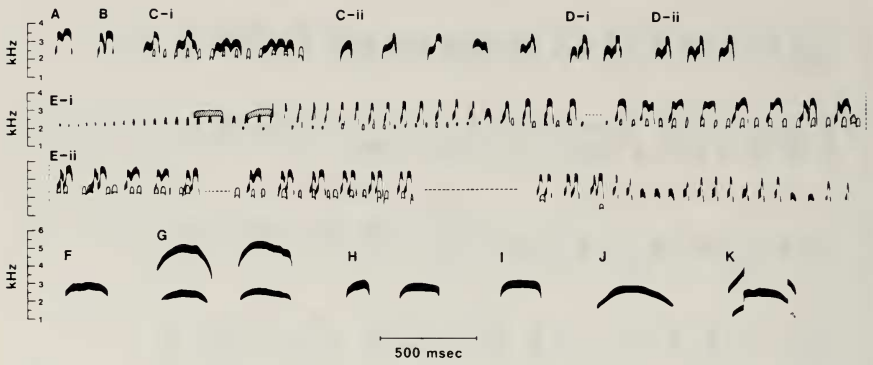


FIG. 11. Ground piping vocalizations of *H. ater* and long calls of *H. ater* and *H. p. palliatus*. (A, B) Piping calls of *H. ater*; (C) partial piping sequence of *H. ater* (i) and single calls from later in that sequence (ii) (intervals shown in C-i can be judged from the time marker; those shown in C-ii are arbitrary); (D) piping calls of 1 *H. ater* (intervals between calls can be judged from the time marker); (E) complete piping sequence of 3 *H. ater* (illegible parts are replaced by horizontal dashes; vertical dashed line indicates where the 2 segments of the sequence are joined); (F) flight call from a pair of *H. ater* after they left a piping interaction; (G) ground calls of a male *H. ater* far from us, when we were near his nest (interval between calls is arbitrary); (H, I) ground (H) and flight (I) calls of a pair of *H. ater* after piping with other birds; they flew to a feeding area (interval between the calls in H is arbitrary); (J) call from a lone *H. p. palliatus*, in an unknown context; (K) call from a pair of *H. p. palliatus* as they flew high over other territories. Only the fundamental frequency of each call is shown, except in G, where the second harmonic contains the most energy and in K (the central part of this call had a weak second harmonic, which is not shown). Analyzing filter band width, 300 Hz.

DISCUSSION

Behavior of adults disturbed near the nest.—Diversionsary displays of *H. leucopodus* near the nest include false-brooding, tail-flagging and crouching with the tail slightly erected or depressed and fanned. False-brooding is widespread in waders, and needs little comment (Hall 1959; MacLean 1972; Simmons 1955; Williamson 1943, 1952). Tail-flagging is the most striking display, and occasionally grades with false-brooding, when the tail may be lifted to various degrees (see Fig. 10 of MacLean 1972). Tail-flagging resembles piping in that the tail is erected and the under-tail coverts are erected and spread, the wings are lifted away from the body, and there is occasional rapid treading of the feet, suggestive of the rapid running that occurs in aggressive piping. It differs in the erect carriage of the head and neck, and in the fluffing and drooping of the wings. The wing component also occurs in a display of nesting Killdeer (*Charadrius vociferus*), when approached by man (see Fig. 2 in Plate III of Simmons 1955), and strongly

resembles the use of wings during brooding in waders. Tail-flagging in *H. leucopodus* may therefore include components of threat display (aggressive piping) and brooding tendency, now ritualized as an anti-predator display.

Crouching with the tail depressed resembles a widespread distraction display in waders (Simmons 1955). This display is weakly developed in *H. leucopodus*, in contrast to some populations of European *H. ostralegus* (Williamson 1943, 1952) and the Chatham Islands (*H. chathamensis*) and Variable (*H. unicolor*) oystercatchers (A. J. Baker, unpubl.). These trends are not related simply to predation intensity. There are no natural mammalian predators on the Faeroes, where distraction display of *H. ostralegus* is very strongly developed, or in the range of *H. chathamensis* or *H. unicolor*. This display is shown weakly by *H. bachmani*, *H. leucopodus* and the South African Black Oystercatcher (*H. moquini*), all of which are exposed to nest predation by mammals (Hall 1959, Webster 1941).

Calls of *H. leucopodus* alarmed near the nest are very different from analogous calls of *H. ater* and *H. palliatus*. These differences are like those between piping vocalizations of the same species, and are discussed below. Calls of *H. ater* and *H. palliatus* are quite similar, and vary from simple short notes to long compound calls. Alarm calls by *H. ater* seem to be more graduated than those of *H. palliatus*, possibly because *H. ater* nests in very high densities (at least at Punta Tombo), a situation allowing information in graded signals to be transmitted (see below). Grading in alarm calls of 1 female *H. ater* is discussed by Miller (1979).

Piping.—Piping probably has similar functions in all oystercatcher species. In European *H. ostralegus* it is predominantly hostile behavior between birds with adjacent nesting territories, but also occurs in many other circumstances, such as when mates meet or in response to fledged young begging for food (Glutz von Blotzheim et al. 1975, Heppleston 1970, Huxley and Montague 1925, Lind 1965, Makkink 1942, Vines 1979). These contexts are similar to those for piping in *H. leucopodus* and *H. ater*. Males of *H. ostralegus* may pipe more than females (Buxton 1939, Glutz von Blotzheim et al. 1975), which may explain why only a few birds vocalize during piping interactions (Huxley and Montague 1925, this study); could these be males most frequently? S. Groves (in litt.) suggests that this is so for *H. bachmani*. Piping clearly functions within the pair-bond (and family?) as well as in territorial demarcation. (Detailed study of piping in at least 1 species is needed for meaningful interpretations.)

Piping in *H. leucopodus* includes several striking visual components, including: wings held slightly out from the body, especially at the carpal flexure; parallel running; vertical tail position with spreading and fluffing of the under-tail coverts; and vertical movements of the head and neck. Many species of birds hold the folded wings away from the body in visual

threat (Tinbergen 1953, many others). In pied *Haematopus* spp. this action also displays the white shoulder bay just above the carpal joint, an important component of visual display in some taxa (Lumsden 1970). Within the Charadriiformes, parallel locomotion appears to be most highly ritualized in the Haematopodidae (Glutz von Blotzheim et al. 1975, Hall 1959, Huxley and Montague 1925).

H. palliatus and *H. ater* occasionally raise the tail for a few seconds during piping, but not vertically, in contrast to *H. leucopodus*. Prolonged vertical erection of the tail also occurs in threat and courtship of calidridine sandpipers (Drury 1961, Holmes 1973, Holmes and Pitelka 1964). In the Least Sandpiper (*Calidris minutilla*) this display further resembles that of *H. leucopodus* in the spreading of the under-tail coverts (E. H. Miller, unpubl.). Erection of the under-tail coverts in *H. leucopodus* may be a ritualized expression of defecation, which occurs commonly in stressed vertebrates (Eisenberg and Kleiman 1972, Simmons 1955:143).

Vigorous false-feeding is common in aggressive piping. This displacement reaction may have become ritualized as the vertical movements of the head and neck of piping birds (Heppleston 1970). Both characteristics of piping appear to be widespread in oystercatchers.

Piping in *H. leucopodus* differs from that of *H. ater* and *H. palliatus* mainly in the prolonged upright erection of the tail and fluffing of the under-tail coverts. The tail is not lifted, or is lifted weakly, in *H. bachmani* (rarely reaching a vertical position, S. Groves in litt., but see Kenyon [1949]), European *H. ostralegus* (Huxley and Montague 1925, Makkink 1942), *H. fuliginosus* and Australian *H. ostralegus* (A. J. Baker, unpubl.), *H. chathamensis*, *H. o. finschi* and *H. unicolor* (Baker 1974).

Vocal components of piping in *H. leucopodus* are even more distinctive. Most, or all other species emit brief piping calls which are relatively wide band: *H. ater* and *H. palliatus*; *H. bachmani* (Webster 1941); European *H. ostralegus* (Glutz von Blotzheim et al. 1975, Huxley and Montague, 1925); *H. fuliginosus* and Australian *H. ostralegus* (A. J. Baker, unpubl.); *H. chathamensis*, *H. o. finschi* and *H. unicolor* (Baker 1974). Nevertheless, individual piping vocalizations of the 3 species we studied are similar in an important respect: all are strikingly similar to alarm calls in the same species. Piping seems to be a highly ritualized form of these calls in its rapid delivery, rhythm and strong grading across adjacent elements. Further support for this interpretation lies in the relationship between grading of vocalizations and nesting density in *H. ater* and *H. palliatus*. Alarm calls of *H. ater* vary from single calls to couplets, triplets, etc., according to level of excitement. This species nests at high densities, which should favor highly aggressive displays with high information content (e.g., through grading). Both characteristics are more pronounced in *H. ater* than *H.*

palliatus: conspicuous call couplets occur in piping of *H. ater*, and these show extensive gradation.

H. leucopodus responds to piping over long distances, and the extremely narrow band width of its vocalizations may be an adaptation for long distance propagation. The allocation of all sound energy to a narrow band width may be most economical evolutionarily (Marten, Quine and Marler 1977, Morton 1975, Wiley 1976), and the spectrum of a narrow band call changes very little over distance, as compared to a wide band call with the same center frequency (Konishi 1970, Smith 1977). In addition, the long duration of piping and alarm calls of *H. leucopodus* provides redundancy which improves chance of accurate reception by listeners. Similar long-range vocal displays occur in other waders: Knot, *Calidris canutus*, (Salomonsen 1950) and *Numenius* spp. (Forsythe 1967, 1970; Skeel 1976, 1978). These species nest at low densities in extensive open habitat, like *H. leucopodus*, and their calls are uttered during high flight displays, which further enhances long-distance transmission. The convergences in length and simple spectral structure of these calls probably arose because frequency characteristics degrade much less over distance than do amplitude characteristics and patterns of frequency and amplitude modulation (Wiley 1976, Wiley and Richards 1978). Such calls should therefore have simple temporal structure because of the unstable attenuation characteristics of open habitats (Marten, Quine and Marler 1977), and should have simple spectral structure if they are used over various or great distances, or both.

Systematic comments.—Piping may be an effective isolating mechanism. *H. palliatus* and *H. ater* have similar piping displays which differ markedly from that of *H. leucopodus*. *H. palliatus* and *H. ater* hybridize frequently where they are sympatric (Jehl, Rumboll and Winter 1973; A. J. Baker, unpubl.), whereas only 1 putative hybrid between *H. ater* and *H. leucopodus* has been reported (Jehl 1978). Interbreeding between *H. palliatus* and *H. leucopodus* has not been reported. Likewise, *H. bachmani* and *H. p. frazari* have very similar "behavior and vocal expressions," engage frequently in piping and hybridize extensively (Kenyon 1949:198).

The systematic position of *H. leucopodus* has not been resolved by morphological studies (Baker 1977; Jehl 1968; Strauch 1976, 1978). Some displays of the species are probably unique, but these just strengthen the view that *H. leucopodus* is aberrant within its family. The systematic value of other displays cannot be judged until a detailed comparative study is done.

SUMMARY

The display behavior of the Magellanic Oystercatcher was studied in southern Patagonia and is described comparatively here. Original observations on *H. ater*, *H. palliatus durnfordi* and *H. p. palliatus* are also included.

Behaviorally, *H. leucopodus* is an aberrant species within the Haematopodidae. Nesting adults have a unique tail-flagging display near the nest, when disturbed by man. Piping birds hold the tail upright and fluff the under-tail coverts, display components which are absent or only weakly developed in other oystercatcher species. Vocalizations of alarmed or piping *H. leucopodus* may also be unique. Most or all other Haematopodidae emit short, wide band calls in both contexts. Analogous calls of *H. leucopodus* are extremely narrow band and often of nearly constant frequency, and are much longer. These characteristics also occur in long-distance epigamic acoustic displays of some other waders which nest at fairly low densities in open habitat.

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LITERATURE CITED

- BAKER, A. J. 1974. Ecological and behavioural evidence for the systematic status of New Zealand oystercatchers (Charadriiformes: Haematopodidae). *Life Sci. Contrib., Roy. Ont. Mus.* 96, Toronto, Canada.
- . 1975. Morphological variation, hybridization and systematics of New Zealand oystercatchers (Charadriiformes: Haematopodidae). *J. Zool., London* 161:357-390.
- . 1977. Multivariate assessment of the phenetic affinities of Australasian oystercatchers. *Bijdragen Tot De Dierkunde* 47:156-164.
- BUXTON, E. J. M. 1939. The breeding of the oystercatcher. *Br. Birds* 33:184-193.
- DRURY, W. H., JR. 1961. The breeding biology of shorebirds on Bylot Island, Northwest Territories, Canada. *Auk* 78:176-219.
- EISENBERG, J. F. AND D. G. KLEIMAN. 1972. Olfactory communication in mammals. *Ann. Rev. Ecol. Syst.* 3:1-32.
- FORSYTHE, D. M. 1967. Vocalizations of the Long-billed Curlew. M.S. thesis, Utah State Univ., Provo, Utah.
- . 1970. Vocalizations of the Long-billed Curlew. *Condor* 72:213-224.
- GLUTZ VON BLOTZHEIM, U. N., K. M. BAUER AND E. BEZZEL. (eds.). 1975. *Handbuch der Vögel Mitteleuropas*. Band 6. Charadriiformes. Akademische Verlagsgesellschaft, Wiesbaden.
- HALL, K. R. L. 1959. Observations on the nest-sites and nesting behaviour of the Black Oystercatcher *Haematopus moquini* in the Cape Peninsula. *Ostrich* 30:143-154.
- HEPPLESTON, P. B. 1970. The function of oystercatcher piping behaviour. *Br. Birds* 63:133-135.
- AND D. F. KERRIDGE. 1970. Sexing oystercatchers from bill measurements. *Bird Study* 17:40-49.

- HOLMES, R. T. 1973. Social behaviour of breeding Western Sandpipers. *Ibis* 115:107-123.
- AND F. A. PITELKA. 1964. Breeding behavior and taxonomic relationships of the Curlew Sandpiper. *Auk* 81:362-379.
- HUXLEY, J. S. AND F. A. MONTAGUE. 1925. Studies on the courtship and sexual life of birds. V. The oyster-catcher (*Haematopus ostralegus* L.). *Ibis* 1925:868-897.
- JEHL, J. R., JR. 1968. Relationships in the Charadrii (shorebirds): a taxonomic study based on color patterns of the downy young. *Mem. San Diego Soc. Nat. Hist.* 3.
- . 1975. *Pluvianellus socialis*: biology, ecology and relationships of an enigmatic Patagonian shorebird. *Trans. San Diego Soc. Nat. Hist.* 18:25-74.
- . 1978. A new hybrid oystercatcher from South America, *Haematopus leucopodus* × *H. ater*. *Condor* 80:344-346.
- , M. A. E. RUMBOLL AND J. P. WINTER. 1973. Winter bird populations of Golfo San Jose, Argentina. *Bull. Br. Ornithol. Club* 93:56-63.
- KENYON, K. W. 1949. Observations on behavior and populations of oyster-catchers in lower California. *Condor* 51:193-199.
- KILHAM, L. 1980. Cocked-tail display and evasive behavior of American Oystercatchers. *Auk* 97:205.
- KONISHI, M. 1970. Evolution of design features in the coding of species specificity. *Am. Zool.* 10:67-72.
- LIND, H. 1965. Parental feeding in the oystercatcher (*Haematopus o. ostralegus* [L.]). *Dansk orn. Foren. Tidsskr.* 59:1-31.
- LUMSDEN, H. G. 1970. The shoulder-spot display of grouse. *Living Bird* 9:65-74.
- MACLEAN, G. L. 1972. Problems of display postures in the Charadrii (Aves: Charadriiformes). *Zool. Afr.* 7:57-74.
- MAKINK, G. F. 1942. Contribution to the knowledge of the behaviour of the oyster-catcher (*Haematopus ostralegus* L.). *Ardea* 31:23-74.
- MARTEN, K., D. QUINE AND P. MARLER. 1977. Sound transmission and its significance for animal vocalization II. Tropical forest habitats. *Behav. Ecol. Sociobiol.* 2:291-302.
- MILLER, E. H. 1979. An approach to the analysis of graded vocalizations of birds. *Behav. Neural Biol.* 27:25-38.
- MORTON, E. S. 1975. Ecological sources of selection on avian sounds. *Am. Nat.* 109:17-34.
- REYNOLDS, P. W. 1935. Notes on the birds of Cape Horn. *Ibis* 5 (ser. 3):65-101.
- SALOMONSEN, F. 1950. The birds of Greenland. Munksgaard, Copenhagen, Denmark.
- SIMMONS, K. E. L. 1955. The nature of the predator-reactions of waders towards humans; with special reference to the role of the aggressive-, escape- and brooding-drives. *Behaviour* 8:130-173.
- SKEEL, M. A. 1976. Nesting strategies and other aspects of the breeding biology of the Whimbrel (*Numenius phaeopus*) at Churchill, Manitoba. M.Sc. thesis, Univ. Toronto, Toronto, Ontario, Canada.
- . 1978. Vocalizations of the Whimbrel on its breeding grounds. *Condor* 80:194-202.
- SMITH, W. J. 1977. The behavior of communicating. An ethological approach. Harvard, Cambridge, Massachusetts.
- STRAUCH, J. G., JR. 1976. The cladistic relationships of the Charadriiformes. Ph.D. diss., Univ. Michigan, Ann Arbor, Michigan.
- . 1978. The phylogeny of the Charadriiformes (Aves): a new estimate using the method of character compatibility analysis. *Trans. Zool. Soc. London* 34:263-345.
- TINBERGEN, N. 1953. The Herring Gull's world. Collins, London, England.
- VINES, G. 1979. Spatial distributions of territorial aggressiveness in oystercatchers, *Haematopus ostralegus* L. *Anim. Behav.* 27:300-308.
- WEBSTER, J. D. 1941. The breeding of the Black Oyster-catcher. *Wilson Bull.* 53:141-156.

- WILEY, R. H. 1976. Communication and spatial relationships in a colony of Common Grackles. *Anim. Behav.* 24:570-584.
- AND D. G. RICHARDS. 1978. Physical constraints on acoustic communication in the atmosphere: implications for the evolution of animal vocalizations. *Behav. Ecol. Sociobiol.* 3:69-94.
- WILLIAMSON, K. 1943. The behaviour pattern of the Western Oyster-catcher (*Haematopus ostralegus occidentalis* Neumann) in defence of nests and young. *Ibis* 85:486-490.
- . 1952. Regional variation in the distraction displays of the oyster-catcher. *Ibis* 94:85-96.

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COLOR PLATE

The color plate Frontispiece of the Magellanic Oystercatcher (*Haematopus leucopodus*) has been made possible by an endowment established by Dr. George M. Sutton.